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# THE NERVOUS GANGLIA OF INSECTS.

I.

LTHOUGH the internal structure of the brain of insects has been the object of numerous and important investigations, among which we must place those of Dietl, Flögel, Bellonci, and Viallanes (who have applied the method of sections to the study of this organ), no attention has as yet been paid to the other nerve-centres of insects, and in particular to the ganglia of the ventral chain. Writers have contented themselves with describing the external form of these ganglia, and their anatomical relations to the other organic parts; but nothing has been done to throw light upon their inward structure. All the knowledge which we have on this subject is very meagre and dates far back to the works of the old writers, who, like Newport, had at their disposal no other means of study than the microscopic examination of organs viewed either transparently or in dilacerated preparations. A method so defective could render but incomplete results, and indeed in many cases erroneous ones.

We have sought to supply this much to be regretted lack of entomological knowledge, by applying to the ventral ganglia of insects the admirable method of sectional cutting, which has brought about such marked advances in contemporaneous zoology.

I need hardly insist on the interest of this research. We shall only remark that all anatomical study bears an unfinished aspect, up to the moment at which we grasp the meaning of the organs which we describe; physiology is a necessary complement of anatomy, it is that which gives to it a meaning. Therefore, when we dissect an

organ, which, as in the case of an insect's brain, is endowed with the most complex psychical properties of which these animals are capable, we find ourselves in the presence of parts whose functions almost entirely escape us. What is, for example, that peculiar organ to which we have given the name of the "pedunculate" body? Anatomists have described with the greatest care its connections and portrayed its external contour; but we cannot discover, or even conjecture its uses. It would be necessary to understand the habits of thought and the feelings of an insect, to be able to assign a rôle to parts so complex and so delicate as those contained within its brain.

The study of the ventral ganglia seems to us to be capable of conducting us to a better result, for in everything that concerns these nerve-masses, physiology is more advanced, and, in all cases, clearer. The ganglia of the thorax, for example, are in the main motory centres; the principal nerves that are sent out from them are to be found in the wings and in the feet; the study of the terrestrial, aquatic, and aerial locomotion of insects has already formed the subject of quite a number of important scientific works; we are now upon well-known ground, and we may hope that it will be possible to establish some connection between the anatomical structure of ventral ganglia and the functions which these ganglia control.

This hope appears to us to be the more legitimate, because we can make use of all the resources of comparative anatomy to work out the problem. If we consider any particular function, for example, that of flying, we notice that in species which resemble each other this function is exercised under totally different conditions; the same organ acquires different uses, and these variations become singularly instructive when we can trace their relationship to the particular structure of a nerve-ganglion. Thus, one of the large wings of the dragon-fly, which is almost like a bird in the range and power of its flight, becomes the elytrum of the beetle; the elytrum is a stiff wing covered by chitinised matter and serving as a protection to a part of the thorax and abdomen. Sometimes the elytrum is used in flying, as in the case of the cockchafer. In other lamellicorn insects, in the *Cetonia* for instance, the elytrum is not used in flight; it merely moves aside so as to allow the second pair of wings to un-

fold. Its rôle becomes still less active in the golden carabus, in *Procrustes*, in *Blaps*, and many other *Coleoptera*, whose two elytra are found on one vertical line, and form but one single and immovable portion; then the second pair of wings disappear; from the physiological point of view, the animal becomes apterous. In another and different order, the order *Diptera*, it is the second pair of wings that undergo an important modification; they cease to be used in flying, and are transformed into an organ of equipoise: they are used for maintaining equilibrium.

All these physiological variations, taking place in the selfsame organ, must in all probability have their counterpart in the internal anatomy of the ganglion that governs the organ, and the comparative study of this ganglion in different species will enable us perhaps to discover the functions of some of its parts. Thus, if we consider by hypothesis, as the nerve-centre of flight, some small lobe which is found occupying this or that place in a thoracic ganglion, the disappearance or modification of this lobe in species not possessing the faculty of flying, might serve to throw additional light upon such an interpretation.

What we have just said with regard to flight is equally applicable to terrestrial locomotion, which also represents in itself many varieties. The typal insect possesses three pairs of feet, whence the name of hexapods, but there are particular species which drop a pair of feet, for instance, the Lepidoptera of the genus Vanessa; in others, the physiological function of the foot varies; in the case of the carrion-beetle (a necrophagus coleopter) it serves as an instrument of tillage, to dig with; for the cricket, the third pair of feet are used for the purpose of leaping; for the Dytiscus, it serves as an oar, We must also bear in mind the curious fact that there exists in the larvæ of certain insects what are called supplementary feet, having only a transient existence and disappearing at maturity; the caterpillar, the larva of the butterfly, has five pairs of supplementary feet. These notable facts demonstrated by comparative anatomy, cannot fail to furnish us with valuable information concerning the functions of the complex organs found in the ganglia of the thorax.

But this is not all. We have not enumerated all the contributions of comparative anatomy to the problem which we are now about to consider; we may make use of the method of comparison without bringing the different types into juxtaposition, but by viewing the nervous system of only a single animal in its entirety. We know in fact that the body of an insect is formed by a definite number of segments, all constructed on the same fundamental plan and arranged in a linear series. Each one of these segments is joined to a nerveganglion, which is all its own and supplies it with sensibility and motility, the two elementary properties of nervous activity. In the course of development, these ganglia have the power of changing their positions; and it is not uncommon to find that the greater number of the abdominal ganglia move up into the thorax; each one, nevertheless, retaining its nerve-relationship to its own segment. Now all the segments of an insect's body are not called upon to play the same rôle; a division of labor has been effected among them with regard to the functions which they are found to exercise: as we have already seen, the ganglia of the thorax are essentially centres of locomotion; in the head, one of the ganglia, the subœsophageal, furnishes the nerves of the buccal portions; the other one, the brain, is connected with particular nerves and becomes the centre of the highest form of psychical activity of which the creature is capable. We have here a number of modifications superadded to the original plan. Yet the original plan should again be met with in the ganglia that have been least differentiated, such as those in the abdominal region; and the comparison between an abdominal and a thoracic ganglion, for instance, is well calculated to show what are the primal and fundamental structures, and what are the secondary ones which have been superadded and have become necessary for the execution of the more complex functions. The study of embryonic and larval forms so easily observed in insects, will most probably conduct us to the same result. And thus perhaps by continuous efforts, all guided by the same governing idea, we shall ultimately arrive at the analogies that exist between the cerebroid ganglia and the humblest ganglia belonging to the ventral chain, and thus finally be able to understand the action of the nerve-substance.

The importance of this object, which, be it clearly understood, can never be attained except by the united effort of many workers, is well calculated to command our strenuous exertions and to encourage us in surmounting the difficulties of a study which is as yet almost entirely new.

II.

We shall restrict ourselves in this article to the consideration of one particular case; we shall describe a single ganglion of the insect. The type we have chosen, for reasons too lengthy to enumerate, is a Coleopter of the family of *Melolonthidæ*; the *Rhizotrogus solstitialis*, a small beetle very commonly found in the southwest of France. We will now proceed to the consideration of the first thoracic ganglion.

The prothoracic ganglion in the rhizotrogus is joined by very short connective filaments to the second thoracic ganglion, and also to the sub-œsophageal ganglion; this latter ganglion, we must note en passant, being situated in the thorax. If with a pair of scissors we sever the head of the rhizotrogus, we find that the remainder of the body contains not only the thoracic ganglia, but also the sub-œsophageal; a peculiarity which, from a physiological point of view, is very interesting.

The ganglion of the pro-thorax, which is greater in width than it is in length, bears a vague resemblance to a cone the base of which is turned towards the sub-œsophageal ganglion, whilst the apex points towards the second ganglion of the thorax. From the lower part spring two large nerves, their starting-point being nearer the ventral than the dorsal surface, a fact clearly comprehended when we find that the fibres of these nerves extend for the most part into the first pair of feet, that is to say, into those organs that lie underneath the horizontal plane of the ganglion. The connective filaments which penetrate the ganglion anteriorly enter it nearer the dorsal surface than the ventral, this last being extremely convex. Dissection throws no additional light upon the anatomy of the gan-

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glion. But by means of a series of sections, we find that it is composed of a mass of fibrillar substance which occupies its centre portion and of a layer of nerve-cells surrounding the fibrillar substance. This fibrillar mass is, owing to its great volume, far the most important, and constitutes in itself alone about four-fifths of the organ. The fibrillary structure can only be satisfactorily analysed by using on it osmic acid, or other equivalent reagents which dissociate it and admit of its being reduced to a certain number of clearly differentiated elements. Whenever osmic acid or a similar reagent has not been employed, or has not sufficiently penetrated the ganglion, owing to the obstacle presented by a thick conjunctival covering or envelope, the fibrillar substance takes on a homogeneous aspect that effectually renders all analysis of it impossible. Everything depends on the employment of a good method of preparation.

When the ganglion has been properly prepared, we perceive a very material difference in the appearance of the fibrillar substance when we compare the dorsal with the ventral region of the ganglion. We can do this very satisfactorily by a longitudinal section, extending through both regions. In such a section close to the median line but not confounded with it (see Cut 16)\* we perceive that the ventral region is occupied by a cord or string of substance which owing to the action of the osmic acid has become very black, and which is formed of so dense a tissue, that we can with difficulty separate it into fibres and fibrillæ. This cord, which, by reason of its position and shape, I propose naming the ventral column, extends over the ventral surface of the ganglion in a longitudinal direction; at both its anterior and posterior extremities it is carried on by fibres extending into the ventral columns of the other ganglia, in such a manner that the entire series of ganglia are united by one continuous ventral cord.

If we look at a transverse section (see Cut 26), the cord, which is recognised by its dark color and by its position near the ventral surface of the fibrillar substance, will be seen to have the form of two almost perfect circles. The ventral column thus presents a circular section, is duplex and symmetrical: there exist two separate

<sup>\*</sup> For the cuts, see the plates in the Appendix of this number.

and distinct ventral columns, separate at least for a certain length; a fact which must be considered in connection with the primitive duality of the ganglion.

In every section where the columns remain distinct from each other, they are separated either by fibres and conjunctival cells, or by nerve-fibres emanating from the cells of the ventral region and proceeding in an upward direction between the two columns. At the other points, the two columns join on the median line. This union is effected in different ways, either by the two columns coming directly together, thus merging into a single mass, or by a commissure which describes the arc of a circle underneath the two columns, or else by the inferior ventral lobule.

We give the name of inferior ventral lobule to a small lobule of fibrillar substance, situated beneath the ventral column. When looked at in a horizontal section not passing through the median line (see Cut 17), this lobule presents the appearance of a rounded protuberance, breaking the almost rectilinear contour of the ventral column. As this characteristic peculiarity is repeated in the internal structure of all the ganglia, we may use it to ascertain the number of the ganglia, whenever these present the appearance of being fused into one compact mass; we may see the practical application of this remark by observing the sub-œsophageal ganglion.

In a succession of horizontal sections, the starting point of which is the ventral region, the first mass of fibrillar substance met with by the knife is the inferior ventral lobule, which is formed (see Cut 1) by two rounded fasciculi, placed symmetrically on either side of the median line and joined together by a transverse commissure.

In these sections, we also perceive fibres of the crural nerve, which, after having extended over a certain length of the ganglion, penetrate into the substance of the inferior ventral lobule (Cut 2). In transverse sections (Cut 23) we find the two ventral lobules placed beneath the two columns which they help to support, and into which they gradually merge; and we also perceive the transverse commissure which joins the two. We shall call this the transverse commissure of the inferior ventral lobule.

Let us now pass on to the examination of the upper surface of

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the ventral column. This surface is covered by a cluster of very fine fibrils rather sparsely disposed; we can clearly follow their course by means of a longitudinal section (Cut 17); we see them again in a horizontal section (Cut 5). To continue the general description of the ganglion we must now consider the dorsal region. It is, as we have previously stated, occupied by a fibrillar substance not so dense as that which composes the ventral column, and we will give the general name of dorsal lobe to this region, reserving the name ventral lobe for the region which embraces the ventral column and its adjoining parts. The dorsal lobe presents as its distinctive characteristic the feature that it is crossed longitudinally by a succession of connective filaments clearly seen in the longitudinal section of Cut 16.

We have already stated that the ventral column receives fibres issuing from the ganglion in front and sends out others to the ganglia in the rear. We shall call the totality of these fibres the connective ventral filaments, and shall call the totality of those that traverse the dorsal lobe the dorsal connective filaments.

The connective filaments which join the sub-œsophageal to the first thoracic ganglion, and which, between these two ganglia, are composed of a dense fasciculus of fibres, distribute these fibres, at the point at which they enter the prothoracic ganglia, in different directions; one set of fibres proceeds towards the ventral column, these are the ventral connective filaments; a second set traverses the dorsal lobe, and are the dorsal connective filaments.

Whilst the ventral connective filaments soon merge into the very dense substance of the ventral column, the dorsal connective filaments, on the contrary, remain distinct from the organs which they traverse, and preserve their individuality throughout. They take directions in three different planes (see Cut 16), consequently they can be subdivided into superior, medial, and inferior dorsal connective filaments.

Newport seems to have observed this distinction of fibres; and he has given the name of sensory column to this first division, and that of motor column to the second. Unfortunately the drawings and figures he has published, though schematically correct, are not clear. We do not adopt his terminology, in the first place

because he designates the organs after their supposed functions, and we have made it a rule never to use controvertible physiological suppositions to designate anatomical organs; and besides, though the name of column is applicable to the connective ventral filaments, we cannot apply it to the connective dorsal filaments, which are subdivided into three pairs of fibrous fasciculi and do not in the least resemble a column.

In the study of Melolontha vulgaris, we have been able to establish in the most absolute manner that there exists a considerable histological difference between the connective filaments of the ventral region and those of the dorsal. Though we have not yet noticed this difference in Rhizotrogus in any marked degree, nevertheless it has seemed to us needful to point it out here, because the fact is of such vast importance that it cannot fail to be general. The dorsal connective filaments, whilst they preserve their individuality in their passage across the dorsal lobe of the ganglion, penetrate nevertheless into some small masses of dotted substance which are found in the path of their entrance into the ganglion. The mass annexed to the inferior dorsal connective filament, is above all very important and is directly connected with the ventral column. As the connective filaments are in pairs, each of these possesses a distinct mass of fibrillar substance and both the masses attached to the same pair of connective filaments are joined by a commissure.

Let us now say a few words about the nerves which proceed toward the prothoracic ganglion. There exists here but one single pair of nerves, extremely important and very extensive. This is the crural nerve. To this nerve are attached the organs which are superadded to the primary structure of the ganglion, such as we have described it, and which in consequence renders the primitive structure more complex. We shall perceive the importance attached to the idea of a *superadded* organ, when we study the abdominal ganglia, where the organs we are about to describe are either completely wanting or are but imperfectly developed.

If now we examine a transversal section taken a little in front of the place from whence the crural nerves emerge (Cut 19), we shall notice that the central part of the ganglion is occupied by the 44 THE MONIST.

ventral column and the upper part by the dorsal lobe. In addition to this, in the lateral regions of the ganglion we find two important masses of fibrillar substance. At this point these two masses remain distinct from the parts we have just mentioned, and on the other hand they are in connection with the crural nerves. The latter send a part, and unquestionably the greater part, of their fibres into the lateral lobes. In a section slightly posterior to the preceding one, also transversal, a very important change has taken place; the two lateral lobules, always connected with the crural nerves, have also established connections with the centre of the ganglion, and in the sections further on the fusion is complete. As these lateral lobules possess the characteristics mentioned, only at the point at which the crural nerves emerge, we shall call them the crural lobes. Thus we find in the prothoracic ganglion three principal lobes: (1) the crural lobe, which is double, symmetrical, and lateral, (2) the dorsal lobe, (3) the ventral lobe. These two last, in contradistinction to the crural lobe, will be classed together under the common term central lobe.

And now to finish this summary description of the prothoracic ganglion, we will point out an important disposition of the connective tissue which divides the ganglion into two halves, one anterior, the other posterior. We can easily understand this disposition by looking at a longitudinal section passing exactly through the median line. From the dorsal surface of the ganglion, may be seen descending a bundle of cells and connective fibres, which, in the form of a column, are directed toward the centre of the ganglion; these cells and fibres do not meet any important organ on their way, the dorsal connective filaments always taking a lateral course. A fasciculus, similarly composed of cells and conjunctival fibres, starting from the ventral surface of the ganglion, appears to meet this conjunctival column (Cut 18). This curious disposition appears to be, as M. Henneguy has ingeniously suggested to me, a trace of the anterior development of the ganglion which had been formed of two distinct portions that have been naturally welded together along the median line; the connective fasciculi corresponding to the point where the welding has been incomplete, and representing the survival of a portion of the walls of the two ganglia.

III.

As the ganglion which we have just described contains some structural difficulties not easy of comprehension, let us proceed with our description under another form, following the order of our illustrations.

Figure 1 is the first horizontal section, cut through the ventral region of the ganglion; the knife has here met the lower ventral lobule, which at this point shows itself double; the two halves being joined by a double transversal commissure. Section 2, made at a point a little higher than the preceding one, shows us at the centre the lower ventral lobule as increased in size; and in the lateral part of the figure appears a new organ, the crural lobule, which is here entirely merged into the lower ventral lobule. The crural lobule is traversed by fibres from the crural nerve, which instead of being entirely lost in its substance, proceed still further, passing into the lower ventral lobule. Section 3 merely brings into prominence an important transversal commissure. In Section 4, the inferior ventral lobule is replaced by the ventral column, which appears double, is symmetrical, and united by a transversal commissure; this commissure being formed of fibrillar substance. The ventral column is closely connected on each side with the crural lobule; it is besides crossed by the ventral connective fibres, which can be seen emerging from its anterior and posterior extremities. Section 5 allows us to examine thoroughly the disposition of those ventral connective fibres; we see that while they penetrate the ganglion, they also pass through two symmetrical masses of fibrillar substance; these two masses, which we name the anterior ventral lobules, are joined together by a transversal commissure. After having traversed the anterior ventral lobules, to which it appears they give a portion of their fibres, the ventral connective filaments pass through the ganglion in an anteroposterior direction, and we see them penetrating the two posterior ventral lobules. The last named lobules, which remind us by their position and appearance of the anterior lobules, receive in addition fibres issuing from the crural lobules; but they do not receive them all, because we notice quite a number of these fibres advancing

directly into the second thoracic ganglion. After emerging from the posterior ventral lobules, the ventral connective filaments pass into the second thoracic ganglion, where we see them penetrate into the anterior ventral lobules.

With Figure 6, we leave the ventral lobe of the ganglion and come to the lower portions of the dorsal lobule. The important filaments crossing this section from the front to the back are called lower dorsal connective filaments. We notice as they proceed some small masses of dotted substance, and, in addition to these, dark colored dots which are the result of the knife having cut crosswise through several fascicles of ascending fibres. We shall find out by means of the sections taken from different parts and placed so as to allow of our better observation, what these ascending fibres are. The crural lobule, always exhibits the same characteristics. We have given it a homogeneous aspect in our drawing. As a fact it presents in its sections a vast number of structural details. But these details being very difficult to understand, we prefer not to dwell upon them.

Section 7 passes through the very midst of the lower dorsal connective filaments; these filaments being in two pairs, one external and the other internal. The external pair, situated somewhat lower, has here disappeared, and the inner pair is the only one to be seen. Some transversal fibres, whose direction appears to me difficult to follow, divide the inside dorsal connective filaments at two different points, and assume the figure of a square; this square has two black dots, produced by the section of the ascending fibres.

A little higher, in Figure 8, the lower connective filaments have disappeared and the fibrillar substance of the ganglion is furrowed by long transversal fibres, of which a part seems to serve the function of joining the two crural lobules, whilst the remainder, proceeding towards the black dots before mentioned, continue their progress with the fasciculi of ascending fibres. These are no other than ascending fibres which, having changed their direction at the plane of the section, proceed almost in a horizontal plane. In Section 9 we follow the course of the medial dorsal connective filaments, separated from the lower connective filaments by the fibres having a

transverse direction, seen in Figure 8. The medial dorsal connective filaments are four in number, an outer pair and an inner pair. At the moment when they leave the prothoracic ganglion, they cross a region where the fibrillar substance is both thicker and darker. In Figure 10 the medial connective filaments are on the point of disappearing; they receive certain fibres coming from the crural lobules, which are now reduced in dimensions. Section 11 shows us the lower dorsal connective filaments, which are the slenderest of all and of which there are but one pair; the crural lobule now disappears. In the middle of the figure, we observe a small collection of conjunctival cells which, as we have supposed, indicates the point where in the course of development the two symmetrical portions of the ganglion have not been perfectly fused together. Finally Section 12 shows two lateral masses of fibrillar substance, separated by a strip of conjunctival membrane.

We will now take up the series of longitudinal sections, the study of which will demand very special attention. We shall there meet again with the organs which we have already examined in the horizontal sections; and we shall perceive that the alterations and modifications presented to us by the difference in our point of observation, bring out very important changes in the appearance of those organs. The sectional method of examination is also one of analysis. In order to reconstruct an organ in its complete form and to conceive of it in space, our mind must bring into a single focus what the sections have represented in a fragmentary manner: we must, in short, substitute synthesis for analysis.

Figure 13 represents the first and exterior longitudinal section; it hardly touches the ganglion; in the front we see the starting point of the crural nerve, and also a portion of the periphery of the crural lobule. The crural nerve exhibits several roots, the most important of which occupy the ventral region. Figure 14, though very elementary, brings out many important points; we see here the crural lobule, which has increased in size and extends from the ventral to the dorsal region; a fact which has already been indicated in the horizontal sections, the crural lobule having been shown in them at all points. This lobule is almost circular in form.

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Along its ventral region, we perceive some of the fibres of the crural nerve which do not penetrate into the lobule; these are the ones we met with in the figures 2 and 3: they are the fibres which pass directly into the lower ventral lobule. With Section 15, we leave the lateral regions of the ganglion and come to the dorsal and ventral regions; we must notice that the crural lobule is continuous with the central fibrillar mass and has no precise limits. In Section 15 the ventral column appears, reduced in size. In the front of it we observe an incisure through which certain nerve-cells send their prolongations into the fibrillar substance.

Figure 16 shows us the complete junction of all the connective filaments traversing the ganglion; first the ventral column, with the connective ventral filaments starting from both its extremities; and then the three dorsal connective filaments, which preserve their individuality distinct, while they cross the dorsal lobe of the ganglion. The lower dorsal connective filament is distinguished from the others by a small compact mass of fibrillar substance through which it We must note that the fibrillar substance becomes thicker at the point where the whole series of connective filaments enter the ganglion, and the same thing is repeated at the place where they leave the first thoracic ganglion to enter into the second. The ventral column is distinguished from the other parts of the ganglion by the dark color which it assumes through the action of the osmic acid; it presents black granules which, examined with a strong lens, show small fasciculi of fibres running in a parallel direction. cells which line the lower surface of the ventral column do not throw out any prolongations; they are exceedingly small, but do not otherwise present any special feature.

Figure 17 is but very slightly different from the preceding one: the ventral column is simply strengthened on its lower surface by the lower ventral lobule. The position of this lobule is interesting to note. We have already mentioned that each ganglion is divided into two halves by a column of conjunctival tissue, one anterior and the other posterior. In Section 17 we see the granulated projection of the ventral portion of this conjunctival column. In order to simplify it we have shown no conjunctival tissue in our illustra-

We may nevertheless notice, that the nerve-cells at the point marked c. c. seem to separate one from the other, and show a triangular space between them, filled with conjunctival cells. segment had not been cut so obliquely, (and this obliqueness in the sections is almost unavoidable when dealing with such very small organs,) we should also perceive on the dorsal line of the section the projection of the dorsal part of the conjunctival column; in fact we shall see this projection in the figure which follows. The presence of the conjunctival column separates, as we have said, each ganglion into two parts, one anterior the other posterior. These portions are not at all symmetrical. We see in Section 17 that the lower ventral lobule is found only in the anterior part. Finally from the ventral column rises an important fasciculus of ascending fibres, which we have already seen in the horizontal diagrams; it is difficult for us to ascertain what these fibres are. In the 18th and last section we approach nearer the median line. The ventral column at this level has the appearance of being divided into two trunks. The ventral connective filaments are clearly seen upon its upper surface. Among the dorsal connective filaments the middle one alone remains visible and receives a certain number of fibres from the ascending fasciculus.

To complete our description let us glance at the series of transverse sections. In Figure 19 the two crural lobules have not yet united and are not yet merged into the dorsal-ventral lobe. This junction does not take place until we come to Figure 20. Here, at this level, we see in addition the circular segment of the two ventral columns, which by their dark color are sharply outlined against the remainder of the fibrillar substance. To the right and left of these two columns we perceive small masses of dotted substance; we merely call attention to them and shall not describe them. Figure 21 furnishes no noteworthy modifications of the preceding. We simply see a few cells of the periphery sending out their prolongations into the fibrillar substance. The point at which they thus penetrate it has already been indicated in Figure 15. In Figure 22 we have a section of several dorsal connective filaments; among others a lower root of the crural nerve is here seen to pass along the ven-

tral surface of the fibrillar substance without penetrating into the crural lobule. Does there exist an upper root of the same nerve, which follows the upper surface of the dotted substance? We do not dare to decide the question. One thing is certain, and that is that if the nerve does exist it is accompanied along its path by a great number of widely ramified tracheæ, of which we see a drawing in tr. In the three figures which follow (23, 24, 25) the ventral column presents an interesting series of modifications. First of all, in Figure 23, it is surrounded by the lower ventral lobule, of which the two masses are in a lateral position, and whose commissures pass underneath the column. We see in the same Figure 23 the two lower roots of the crural nerve, advancing towards the column. In the 24th section the two roots have reached the column, and two other nerves cross the crural lobule; doubtless their destination is the lower dorsal connective filaments, but of this we have no clear indication. In the 24th section two other crural roots also enter the lower ventral lobule. This section is very favorable for the examination of the ascending fasciculus which we have already noticed in the longitudinal sections. It seems to us certain that this fasciculus terminates in the middle dorsal connective filament. Its origin is more uncertain. It seems to spring from the ventral column, or else to come from crural roots which, after having traversed the crural lobule, reascend towards the dorsal lobe of the ganglion, describing a curve exteriorily concave. It is possible that this ascending fasciculus has both these origins. The 26th and last section shows us the ventral column on a larger scale; the two columns being distinct from each other, though united at the lower extremity by a commissure. The ensemble of the figure strikingly reminds one of a section of the abdominal ganglion.

Here our description ends. We have not sought to follow up every fibre in all its details, nor to describe completely the anatomy of each organ. Our intention has merely been to give a synthetic notion of a nervous ganglion. Subsequent studies made on other ganglia will demonstrate the general application of this idea.

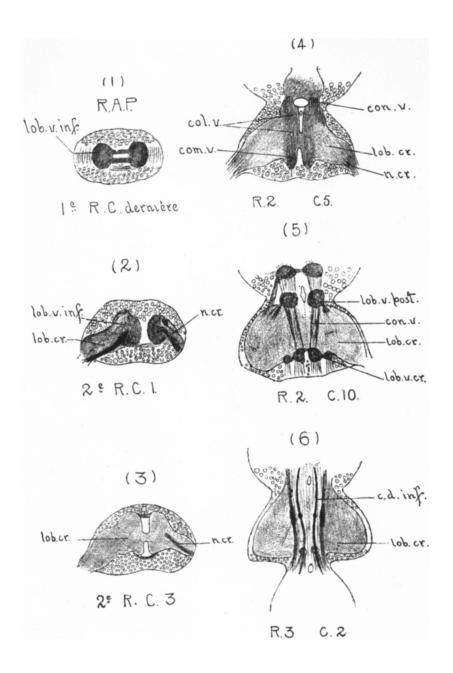
## APPENDIX.

# PLATES BELONGING TO THE ARTICLE "THE NERVOUS GANGLIA OF INSECTS."

#### KEY TO THE PLATES.

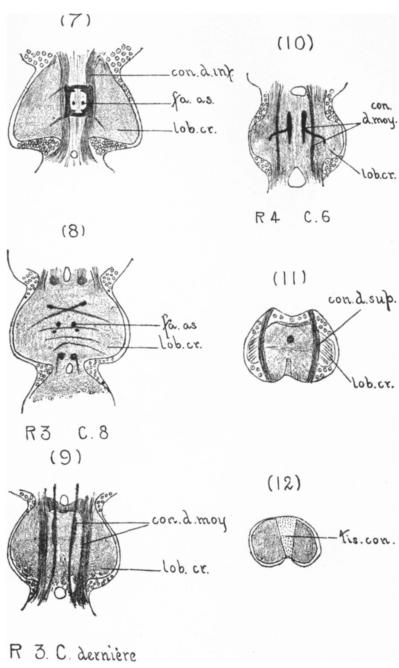
- col. ven.-ventral column.
- lob. dors.—dorsal lobe.
- lob. ven.-ventral lobe.
- lob. v. inf.—inferior or lower ventral lobule.
- lob. cr.—crural lobule.
- con. dors. sup.—superior (or upper) dorsal connective filaments.
- con. dors. moy.-medial dorsal connective filaments.
- con. dors. inf.—inferior (or lower) dorsal connective filaments.
- con. v.-ventral connective filaments.
- n. cr.—crural nerve.
- n. al.—alary nerve.
- lob. al.—alary lobule.
- rac. sup.—upper (or superior) root.
- rac. moy.-medial root.
- rac. inf.—lower (or inferior) root.
- fa. as.—ascending fasciculus.

## PLATE 1.



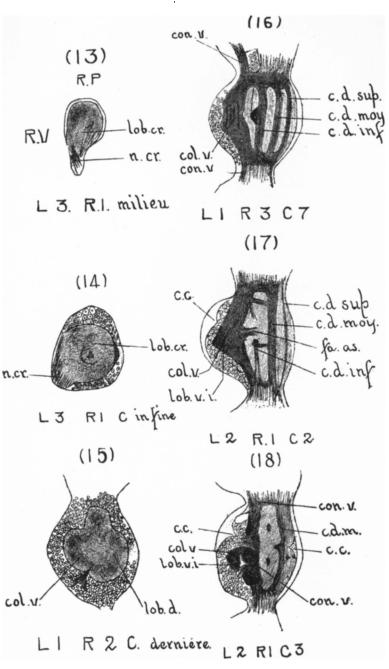
Rhizotrogus solstitialis. First thoracic ganglion. (Horizontal sections.)

## PLATE II.



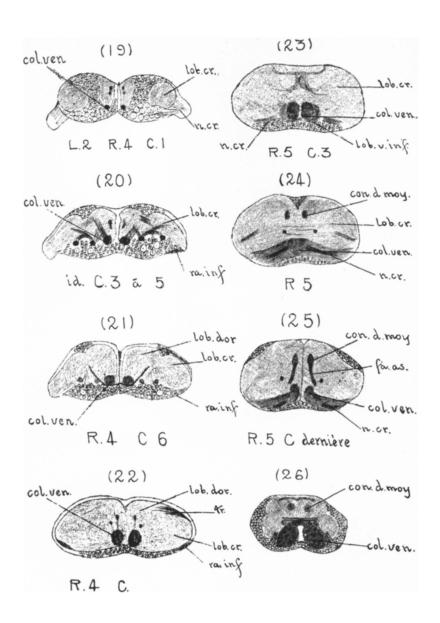
Rhizotrogus solstitudis. First thoracic ganglion. (Horizontal sections.)

## PLATE III.



Rhizotrogus solstitialis. First thoracic ganglion. (Longitudinal sections.)

## PLATE IV.



Rhizotrogus solstitialis. First thoracic ganglien. (Transversal sections.)